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THE BIOGENETIC LAW FROM THE STANDPOINT OF PALEONTOLOGY.

THE interest of the paleontologist in embryology, and in ontogeny in general, lies wholly in the wish to know the origin and relationships of biologic groups; a scientific interpretation of ontogenic data in terms of phylogeny depends on the extent of preservation of the ancestral record in individual development. The broad statement has often been made that each animal gives in its own development an epitome of the history of its race. Because of the law of heredity, this statement would be true, and the record would be complete, if nothing had interfered with the normal course of things. But, in reality, so many secondary elements are introduced in development, that authorities are very much divided as to the value of ontogenic stages as records of race history.

There can be no doubt that students of postembryonic stages have been inclined to claim too much for the law of tachygenesis, while, on the other hand, students of embryology have been inclined to discredit it almost entirely, and to lay little stress on ontogenic stages as a recapitulation of phylogeny. The reason for this disagreement is not far to seek; it lies in the field and in the methods of research of the two groups of morphologists.

Types of development.—Leaving out of consideration the *Protozoa*, which come into being with the essential characteristics of the adults, there are, in the *Metazoa*, two types of development: (1) the *fœtal type*, in which the development takes place in the egg, or in the body of the parent, and the young animal comes into the world in form closely resembling the adult; (2) the *larval type*, in which the young animal comes out at an earlier stage of development, and reaches maturity only after considerable metamorphosis.

Secondary elements will be introduced in either type of development, and those variations that are favorable to the preservation of the species are likely to be perpetuated by heredity. Now in the fœtal type the most favorable variation consists in abbreviation, thus simplifying the development. Any characters that are useful in a free state, but not in a fœtal state, are liable to be lost. Thus in the fœtal type the tendency is toward loss of the record through omission of stages or obscuring them, for many organs that would be highly developed in mature forms, or in free larvæ, will be either suppressed or undifferentiated.

The vertebrates, most of the higher crustaceans, most land and fresh-water mollusks[1] have the fœtal type of development; and these embrace by far the larger part of animals whose ontogeny has been studied. It is not to be wondered at, then, that morphologists who deal exclusively with embryonic stages of these groups should be skeptical about the repetition of family history in individual development. Here many stages are omitted, and the rest so obscured and undifferentiated as to be unintelligible; and secondary characters, due to life in the egg or in the parent, are introduced, effacing what little meaning was left. Then, too, embryologists are often content to trace the animal but a little way toward perfection of development; they study the embryo until the cells begin to divide into groups indicating a beginning of organs, and call this studying ontogeny, when they have stopped before it could be told whether the animal was going to develop into fish, flesh, or fowl. To this sort of study is due the idea of "falsification of the record," a crime of which nature has not yet been guilty, although she at times may not, perhaps, have told the whole truth.

Primary and secondary larvæ.—If the way of the embryologist lies in stony places, that of the student of postembryonic stages is not much smoother; formidable obstacles meet him on every side, reducing his small stock of faith. At the very outset he is confronted by the difficulty that there are two distinct types of larvæ: (*a*) *primary larvæ*, such as are more or less modified from ancestral forms, and have continued to develop as free larvæ since the time when they constituted the adult forms; (*b*) *secondary larvæ*, such as have been introduced by cenogenesis into the ontogeny of species that formerly developed by the fœtal process. If ancestral characters have been retained in the egg, then these secondary larvæ may bear some palingenetic characters, and thus be hard to distinguish from primary larvæ; otherwise they will be entirely adaptive, or cenogenetic. A case in point is the development of most insects, whose larval stages are supposed to be largely secondary. Study of individual development in a group of this sort can throw little light on phylogeny.

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[1] *Dreissensia*, a fresh-water pelecypod, which in very recent geologic time has immigrated from salt water, still goes through its larval development, like its marine relatives.

The student of larval stages must confine himself to the primary sort, if he would correlate them with ancestral genera. The development of the cœlenterates, echinoderms, brachiopods, most mollusks, and the lower crustaceans is direct; thus larval stages of these groups may be bearers, to a greater or less degree, of ancestral characters. But since the free larvæ of even these groups are exposed to natural selection, secondary or cenogenetic characters will be introduced, obscuring the resemblance to ancestral forms; also characters that in the adult ancestral form were functional and fully developed may, in the representative larval stage of the descendant, be so little differentiated as to be unrecognizable.

But how can the morphologist who deals entirely with living species know whether a character is primary, and repeated by palingenesis in the larval history of the descendant, or whether it is secondary, and introduced by cenogenesis into that history? The answer to this lies wholly within the domain of paleontology, for only by finding a stage of growth represented by an ancestral form can the morphologist know that the characters of that stage are ancestral, and not secondary. Larval stages which may be the bearers of ancestral characters must then be compared with the adults of their predecessors, and the paleontologic record must be invoked as a final resort — the court from which there is no appeal.

And this was exactly the method used by Louis Agassiz, who first applied the law of acceleration of development to the study of systematic zoölogy, although it never had much influence on biologic investigation until the palentologic studies of Hyatt in the invertebrates and Cope in the vertebrates placed the law on a sound basis. It was reserved for Alpheus Hyatt to formulate the law and to strengthen theory with practical examples based on study of cephalopods. In his later papers Professor Hyatt[1] has given a more exact and comprehensive definition of the law of acceleration or *tachygenesis:* "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of acceleration, until they either become embryonic or are crowded out of the organization and replaced in the development by characteristics of later origin." A still more definite statement by the same author is the following: "The substages of development in ontogeny are the bearers of distal ancestral characters in inverse proportion and of proximal ancestral characters in direct proportion to their removal in time and position from the protoconch, or last embryonic stage."[2]

To insure trustworthy results in verifying this law, the investigator must have groups in which the larvæ are primary and reproduce ancestral characters; in which the living and the fossil are classified on the same basis; of which we have preserved a nearly complete geologic record, and of which material is available for the study of fossil ontogeny as a check on the living. Such groups are especially represented among the *Cœlenterata*, the *Echinodermata*, the *Brachiopoda*, and the *Pelecypoda* and *Cephalopoda* among the mollusks.

Unequal acceleration.— Now, when the morphologist has settled the fact that primary larval stages do actually reproduce, more or less vaguely, characters that existed in the adult forefathers of the generation he is at work on, his troubles are even then not yet ended; for the characters do not necessarily appear in the ontogeny of the descendant in the same association in which they occurred in the ancestor. A character useful to the immature form will have a tendency to be inherited at an earlier age than those useful only to the adult, and so by unequal acceleration of development the parallel between ontogeny and phylogeny is broken. It was once thought that the *Nauplius* larva of the crustaceans was a mature genus, then it was thought to be a larval representative of the extinct radicle of the Crustacea; later still, many morphologists have concluded that the *Nauplius*, while it bears many crustacean characters, still retains too many annelid characters to represent the radicle of the group; it is a typical crustacean larva, but not a representative of the primitive crustacean, and the two sets of characters are thrown together by unequal acceleration. Beecher has shown the same thing in the spiny larvæ of *Acidaspis* and *Arges*, where in the protaspis of these genera the spines characteristic of the adults appear, contrary to usage among the trilobites, in which larval stages are usually smooth. Thus before these animals have assumed characters that would identify them undoubtedly with trilobites they have assumed those most characteristic of their own genera. Jackson has shown that in the larvæ of the *Pectinidæ* unequal acceleration may associate characters that were not synchronous in race history. F. Bernard has recently shown that the prodissoconch of pelecypods is sometimes striated and ribbed, characters that could not have belonged to the primitive pelecypod.

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[1] Genesis of the Arietidae, p. 9.

[2] Philogeny of an Acquired Characteristic, p. 405.

If unequal acceleration causes confusion in the phylembryonic stages, the difficulty is much greater in the larval and adolescent periods, where the shortness of the time of development causes throwing together of characters that were not contemporaneous in the ancestors, and where the small size and general habits prevent differentiation of organs that in the correlative adult forms were highly developed, thus obscuring and even destroying the exactness of the parallelism. Two species of *Placenticeras*, of which the ontogeny has been recently studied by the writer, must have descended not only from the same perisphinctoid family, but also from the same species of *Hoplites;* and thus, if the parallel were at all exact, they should be alike in the late adolescent stages when they begin to show their generic characters. This, however, is not the case, for they are quite different throughout the cosmoceran stage, and back almost to the end of the larval period, where the transition from goniatite to ammonite took place. If this were interpreted without taking account of unequal acceleration, it would seem that the differentiation of the two species took place back in the Trias, and that different ægoceran forms were the remote ancestors of the two species, which we know could not have been the case.

The writer has recently worked out the ontogeny of two very nearly related species of *Schlœnbachia*, one of which, in its larval period, reproduces very exactly a *Paralegoceras* stage, while the other does not ; the latter species has, however, all the paralegoceran characters, but associated with others that this genus never had, but which belonged to later descendants of this genus. There can be here no question of the veracity of nature in keeping the record, the difficulty lies in deciphering it. So it is not to be expected that any one species would give in plain terms the complete phylogeny of a genus, for stages that are plainly differentiated in one will be obscured in another, and only by studying the ontogeny of a number of species of one genus can the morphologist hope to get a complete history. It is still less to be expected that two separate genera, even when closely related, should tell their story in exactly the same terms, for stages that are emphasized in the ontogeny of the one are obscured and possibly even omitted in the other. And in this case the unequal acceleration goes much farther than with closely connected species. In a comparative study of *Lytoceras* and *Phylloceras* the writer[1] has recently shown how rapid this divergence is, and has drawn the conclusion that unequal acceleration would account for a large part of the differentiation observed in successive geologic generations.

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[1] The Development of *Lytoceras* and *Phylloceras*. Proc. Calif. Acad. Sci., Third Ser. Geol., Vol. I, No. 4, 1898.

Retardation.—Another factor that makes it difficult to correlate ontogeny and phylogeny is *retardation* of development. Cope first recognized the principle, but in his writings confused it with unequal acceleration, and since his reasoning was purely theoretical the idea has never gained much foothold in biologic philosophy. Cope's[1] statement of the theory is as follows: "The acceleration in the assumption of a character, progressing more rapidly than the same in another character, must soon produce, in a type whose stages were once the exact parallel of a permanent lower form, the condition of inexact parallelism. As all the more comprehensive groups present this relation to each other, we are compelled to believe that *acceleration* has been the principle of their successive evolution during the long ages of geologic time. Each type has, however, its day of supremacy and perfection of organism, and a retrogression in these respects has succeeded. This has, no doubt, followed a law the reverse of acceleration, which has been called *retardation.* By the increasing slowness of the growth of the individuals of a genus, and later assumption of the characters of the latter, they would be successively lost." This statement of Cope might apply equally well to unequal acceleration of characters, but in another part of this same work he gives a clearer statement: "Where characters which appear latest in embryonic history are lost, we have simple retardation, that is, the animal in successive generations fails to grow up to the highest point of completion, falling further and further back, thus presenting an increasingly slower growth in the special direction in question."[2]

These remarks of Cope were based on abstract reasoning, but it is possible to bring up some striking cases in support of the theory, notably among the brachiopods. Fischer and Oehlert[3] have shown that while brachiopods go through many metamorphoses in individual evolution, and while each species is usually constant in the stages it goes through, it often happens that the individual is arrested in development, never reaching the full generic development of the mature stage. The individual then begins to reproduce its kind before maturity is reached, and tends to give rise to a stock that never reaches the full generic evolution of its ancestors. Dr. C. E. Beecher has well described this: "In each line of progression in the Terebratellidæ the acceleration of the period of reproduction, by influence of environment, threw off genera which did not go through the complete series of metamorphoses, but are otherwise fully adult, and even may show reversional tendencies due to old age; so that nearly every stage passed through by the higher genera has a fixed representative in a lower genus. Moreover, the lower genera are not merely equivalent to, or in exact parallelism with, the early stages of the higher, but they express a permanent type of structure, so far as these genera are concerned, and after reaching maturity do not show a tendency to attain higher phases of development, but thicken the shell and cardinal process, absorb the deltidial plates, and exhibit all the evidences of senility.[1]

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[1] Origin of the Fittest, p. 142.

[2] Op. cit., p. 13.

[3] Brachiopodes, Mission Scientif du Cap Horn, p. 50–60.

If, then, the morphologist tries to study the race history in one of these species thus arrested in development, he cannot read the whole story, for the individual ontogeny will not recapitulate the higher stages lost by retardation.

Another remarkable case is that of the so-called "ceratites" of the Cretaceous. While there have been no goniatites since the Paleozoic, and no ceratites since the Trias, there are found among the ammonites of the Cretaceous some with septa of simple goniatitic character, and others with septa like those of the genuine ceratites. Now since the line of descent is broken, and there is no possibility for a continuous line of these ancient primitive forms to have bridged over the great gap from the Trias to the Upper Cretaceous, we must explain this either by reversion or in some other way. But it is not a simple case of reversion, for, as has been pointed out by several writers,

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[1] Amer. Nat., Vol. XXVII, 1893, p. 603.

Douvillé, Nicklès, and others, the septum of adolescent ammonites of this group is not more complex, but really less so, than that of adults, although they are derived from Jurassic genera with complex septa. Thus Douvillé derives the group *Placenti ceras-Sphenodiscus* from *Hoplites;* the Pulchellidæ, composed of *Pulchellia*, *Neolobites*, and *Tissotia*, he derives from *Oppelia* of the Jura. Since in each case the ancestral forms are more complex than the descendants, the reduction in complexity of generic evolution can be explained only by retardation or arrested development. F. Bernard has in addition pointed out the fact that the adult of *Pulchellia* is like the adolescent stage of the ancestral *Oppelia.* Now if we define the law of acceleration of development to mean that in a progressive series the young of the descendants correspond to the adults of their more remote ancestors, we find that this does not apply to a retrogressive (retarded) series. In this latter case we must restate the law as follows: the adults of descendants correspond to the young of their more remote ancestors, the higher generic stages to which these ancestors attained having been dropped away by successive retardation or arrested development. The retarded series themselves may become the radicals of new stocks, and so we may have cases where the ontogeny of any one species or genus can never give the full history of the race.

Groups available for correlation.—We see then that the student of morphogeny of animals has to be on his guard, first against the loss of generic stages during the period while the animal is in the egg; then against the introduction of secondary larval stages when the ancestors lacked them; then against the introduction of secondary characters due to adaptation; then against unequal acceleration, bringing together in the ontogeny of the descendant, characters that occurred in separate generations of ancestors; and lastly, against retardation, by which the form never reaches the full generic evolution of its ancestors, and where, if a new series starts out from the retarded form, the complete family history is not recorded in ontogeny.

Is it to be wondered at, then, that the student of morphology becomes a sceptic, or even a rank unbeliever with regard to the value of ontogenic stages as records of history? It is only to be expected that the biologist, especially one that deals almost exclusively with living species, should be inclined to discredit the law of tachygenesis, and to believe that there is such an inextricable muddle of omissions, secondarily introduced characters, and unequal acceleration of those actually repeated, that the record is wholly untrustworthy, or at least illegible. And yet there are so many species and genera in the various groups of invertebrates whose ontogeny is simple, progressive and fairly complete, and whose stages of growth are almost exact repetitions of successive antecedent genera, that it would be impossible to find a student of the morphogeny of the brachiopods, the marine mollusks, or the lower crustaceans, that does not believe implicitly in the value of larval stages of these groups as records of their family history. And this is especially true of the paleobiologists, who regard it of little importance whether the animal under investigation died yesterday, during the flood, or during the Paleozoic era, whether it is preserved in alcohol or in a more permanent museum in the bosom of mother earth; they recognize the fact that the life-history of a Cambrian trilobite has as much bearing on modern biology as does the history of the living crayfish, and that the laws that govern the rise and decline of organisms were just as true then as now.

Not all groups are equally useful to the student of morphogeny, but in each of the lower subkingdoms there are genera of which the ontogeny has been studied and correlated in no uncertain terms with the history of the race. The testimony of these various groups is so uniform, notwithstanding the fact of its having been gathered by men of different beliefs, that its value cannot be doubted. It is also noteworthy that in the higher groups, such as cephalopods and crustaceans, the evidence and the correlations are much more decided.

Cœlenterata.—It has been shown by Dr. C. E. Beecher that the young stages of the Favositidæ correspond to *Aulopora*, or to some other similar unspecialized genus. This same conclusion has been reached by Dr. G. H. Girty based on a study of the ontogeny of *Favosites*, *Syringopora*, and other tabulate corals, all of which are shown to go through an *Aulopora* stage of growth.

Echinodermata.—The only crinoid of which the ontogeny is known is *Antedon*, which has been shown by Sir Wyville Thomson to go through successively stages corresponding to the *Ichthyocrinoidea* of the Paleozoic, and *Pentacrinus* of the Mesozoic, before it becomes free swimming and takes on the characters of *Antedon*.

Dr. R. T. Jackson has been able to prove even in the Paleozoic sea-urchins the possibility of correlating growth stages with phylogeny, in spite of the great difficulties due to resorption of plates, and change of form.

Brachiopoda. — According to Beecher all brachiopods go through a primitive protegulum stage, correlative with the supposed ancestor of the class, although *Paterina*, which was formerly supposed to be this radicle, has been shown to be much more highly specialized than the protegulum stage. The later stages of growth of this class are capable of even more remarkable correlation, as has been shown by Beecher in a number of papers, where every stage of growth is distinctly homologous with well known pre-existing genera; and these same successive genera show a gradual transition in the adults.

Even among the Paleozoic spire-bearers (*Helicopegmata*), this holds good, for Beecher and Schuchert have demonstrated that the early stages of this group are homologous with the terebratuloids (*Ancylobrachia*), aud more especially with the Paleozoic genus *Centronella*, the most primitive of the loop-bearing brachiopods.

Mollusca.—Jackson's correlations of the stages of growth of pelecypods with their race history have already become classic; according to these, every pelecypod begins its bivalve state with a nuculoid stage, homologous with the primitive radicle of the group. Every *Pecten* goes through stages successively correlative with a nuculoid, *Rhombopteria*, *Pterinopecten* and *Aviculopecten* before it reaches maturity, each stage appearing in the order of the ancestral genus. Even the greatly modified oyster shows its kinship with this group by its nuculoid and *Rhombopteria* stages.

The researches of Branco have made it clear that each group of cephalopods has its typical phylembryo, in a general way correlative with the radicle of the group, and that the later stages may be compared very accurately with ancestral families and genera. The way for this was opened by Hyatt's memoirs on the ontogeny of the ammonites, in which it was shown that in each perfect adult ammonite shell the complete individual ontogeny is recorded. By using this same method Karpinsky has been able to correlate the ontogeny of *Medlicottia* and *Pronorites* with successive ancestral forms, from *Anarcestes*, *Ibergiceras*, *Paraprolecanites*, up to the adult stage.

By the ontogenic method Buckman has been able to get at a sound basis of classification of the Jurassic ammonites, and to correlate the growth stages of many of these with their race history. Although his conclusions as to the systematic position of many of these genera do not agree with the ideas commonly accepted concerning them, it must not be forgotten that these conclusions are based, not merely on ontogenic study alone, but also on the gradual transitions of a series of adults. This is the strongest confirmation that any phylogenic research could ever have.

Crustacea. — Among the most convincing morphogenic researches are Beecher's studies in the ontogeny of the trilobites, all of which are shown to go through a phylembryonic *protaspis* stage, correlative with the primitive crustacean, and similar to the protonauplius of the less specialized living crustaceans. Here, too, it was demonstrated that the larval and adolescent stages of Devonian, Silurian, and even Cambrian trilobites may be correlated with the adults of preëxisting genera, giving the basis of a natural, or biogenetic, classification of this extinct group.

Many more cases might be added to those cited here, but surely no additional evidence is needed, for all this points in the same direction, whether gathered by believers in or opponents of the theory of evolution. To this latter class belong the evidence brought forward by Barrande in the ontogeny of trilobites, and by Agassiz in the law of recapitulation or acceleration of development. Each of these naturalists used unhesitatingly the method that in the hands of Hyatt and his followers has been so fruitful of results.

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